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VASCULAR ANATOMY OF THE SEEDLING OF *MICROCYNAS CALOCOMA*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 122

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(WITH PLATES V AND VI)

HISTORICAL

DECANDOLLE (5) in the first account of the genus *Microcynas* expresses the opinion that it holds a position among cycads intermediate between *Dioon* and *Zamia*.

A historical sketch of the literature concerning *Microcynas calocoma* may be found prefacing the taxonomic account of the species by CALDWELL and BAKER (1), who succeeded in procuring material from Cuba. The only part of their description which concerns us here is the statement that the stem has a single vascular cylinder.

In a second paper, intended primarily to present the conditions in the reproductive structures, CALDWELL (2) has described incidentally some of the superficial characters of the embryo and seedling. Certain details, which he naturally overlooked in so comprehensive a work, have been brought to light by a more detailed study having the seedling alone as its object.

INVESTIGATION

In the first place, it is not the root which is seen to emerge from the seed and bend downward, as described and pictured by this author; the sequence of events in the process of germination is the same as that described for *Ceratozamia* (7), the same which occurs in the other cycads which I have germinated, *Dioon edule*, *D. spinulosum*, and species of *Zamia*. The root is not yet formed when the base of the elongating embryo ruptures the seed coat in the small, less indurated, micropylar region. When it emerges, it still bears the small brown disk constituting the only remains of the coleorhiza, an organ which, in the early stages of the embryogeny, is by far the larger portion of the sporophyte. The united cotyledonary stalks bend downward toward the soil. The root may not pierce the coleorhizal disk until the latter

has touched the soil; indeed its appearance in some seeds is preceded by the exit of the plumule.

A second detail in which this description must differ from the one cited is that the usual number of cotyledons is only two. They never wholly emerge from the seed. Their common stalk, which forms a sheath about the plumule, is soon ruptured in many places by the radial growth of the latter, and its decay causes the seed to drop away.

The appearance of embryos of *Microcycas*, like those of *Ceratozamia* described by CHAMBERLAIN (3), examined at short intervals during the period between fertilization and germination, indicates that there is no resting stage; and if at any time the seeds are allowed to dry, the embryos are killed. LAND (10) relates that he has reason to suspect the same condition in *Ephedra*.

CALDWELL has called attention to the adhesion of embryo to endosperm. This adhesion is greater than in any of the cycads I have studied, except *Zamia*. So intimate is the union, that by using ordinary precautions, one does not separate them entirely, but always carries some few layers of the endosperm through the microtome and stains with sections of the embryo.

Coincident with the close adhesion of embryo to endosperm is the remarkable fusion of the cotyledons. Although these always arise as two distinct organs, the fusion in older embryos is so complete that several were sectioned from the apex to within a distance of 0.5^{mm} above the tip of the plumule without discovering any trace of the characteristic seam made by the meeting of the adaxial epidermal layers (*fig. 1*). The epidermal cells themselves disappear in many cases slightly above the meeting of the inner faces over the plumule. The seam was not seen to extend to the surface at any level in these embryos, although there were conspicuous superficial sutures (*fig. 1*) in some of them. The plumule is liberated by the splitting of the sheath into strips, each of which simulates the petiole of an individual cotyledon. To my knowledge so complete a fusion of cotyledons has not been reported of a cycad.

Each cotyledon may have eight or ten vascular strands; all are collateral, with normal orientation. Apparent exceptions may occur immediately above a dichotomy or immediately below a fusion or an

approximation. In these situations, the xylem of one strand faces that of the other, giving to the inner one an inverse orientation (*d*, *figs. 1, 2*). When the fusion of two bundles is complete, the combination presents the appearance of a single concentric strand.

All the cotyledonary traces are derived from the branching of three, which join the central cylinder (*fig. 3*) in a manner similar to that described by MATTE (11) and THIESSEN (12) for *Dioon edule*, and by the present writer (7) for *Ceratozamia*. The wood remains endarch as far out as the sheathing base of the cotyledons (*fig. 13*); it becomes mesarch in this region; and in the upper portion of the blade the wood in the greater number of the strands is exarch. Transfusion tissue is abundant, and in close connection with the centripetal xylem. Mucilage ducts alternate with the cotyledonary traces. Tannin cells are conspicuous in the peripheral region.

The hypocotyl has no vascular plate, no protostele; the passage from stem to root is therefore easily studied. The four cotyledonary strands remain distinct throughout this portion of the axis, only fusing laterally with the few elements of the leaf traces still remaining to form a very imperfect siphonostele. Their elements finally unite with those of the four root poles. The metaxylem and phloem divide, as usual, and the resulting portions swing to right and left, the right half of the phloem of each joining with the left half of that of the next, with sometimes the lowermost extremities of leaf-trace phloem intervening (*fig. 4a*). There is thus produced the characteristic root structure, four groups of phloem alternating with four double-fan-shaped xylem groups. Irregular proliferation of the medulla often separates the phloem group again into its two constituents (*fig. 6*).

In the cortex of the hypocotyl were discovered the remains of a very broken zone of cambium. No traces, however, of any vascular tissue could be detected outside the central system in seedlings with two expanded leaves and several others developing.

The root in all the seedlings under observation was tetrarch (*figs. 4a, 6*) with a reduction to triarch toward the tip, in some cases. Mucilage ducts are numerous in the hypocotyl, but do not penetrate into the root. Neither pericycle nor endodermis is distinct in these

young roots. The root tip differs in no observable respect from that of *Ceratozamia*.

In the stem four large groups of leaf traces alternate with the cotyledonary strands, just above the cotyledonary node (*fig. 3*). Higher up (*fig. 7*), they close in, and together constitute the central cylinder of the axis. Taking a generally vertical course, these traces branch and anastomose until they reach a position so near to the growing points of leaf and stem that the vascular tissue is still procambial. In this position, even before the procambial strands from leaf and stem apex have united, the traces destined for the leaf margins manifest the phenomenon of girdling.

At first the wood of the leaf traces is endarch. *Fig. 8* represents a portion of a leaf-trace girdle, and *fig. 9* a cross-section of two vertical strands from the middle of the same leaf at the same level. *Figs. 10, 11* illustrate stages in the transition from the endarch to the mesarch condition. The wood becomes exarch at a relatively low level in some of the foliar strands, and there is considerable irregularity in different traces in this respect. *Fig. 12* is a drawing of one of the traces (*b*) in *fig. 14*, still in the region of the stipules. The other traces of the same leaf retain, at this level, a few elements of centrifugal xylem; this strand is entirely destitute of them. Further—and I have attempted to represent it diagrammatically—the wood in all the traces of this petiole is more nearly exarch than in those of the older leaf (*l*²), although the section of that leaf which is here represented is higher up in the petiole than that of the younger leaf. In spite of such irregularities, however, the statement holds that the xylem is entirely centrifugal near the base of both cotyledons and leaves, and that it gradually diminishes to the vanishing point in proportion to the appearance and increase of centripetal xylem in the ascent of the cotyledonary blade and leaf petiole.

The section represented by *fig. 13* is very close to the leaf bases. It shows the increase in the number of bundles entering consecutive leaves, and also the meriphyte's gradual assumption of the Ω arrangement from the open arch of the early leaves. Transfusion tissue is present in these traces.

The strands are all collateral. Frequent branchings and approximations occur, and real fusions are common, most noticeably of those

strands which are brought to the center of the meriphyle and form the flanks of the Ω . When two of these strands are fusing, the centripetal elements of both xylem groups are gradually eliminated and the protoxylem groups are therefore brought together and finally united. This common group of protoxylem, then, is surrounded by the united metaxylem, and outside of this the phloem of both bundles may almost encircle the xylem, completing the delusion of a concentric bundle (*figs. 15, 16*).

Mucilage ducts occur in stem and leaves. They sometimes extend through the petiole as far as the bases of the pinnae.

The characteristic cycad ramentum is prominent, especially upon the unfolded leaves. The hairs are one-celled. *Fig. 18* shows the tip of a young pinna bearing these epidermal outgrowths.

Tannin cells occur in the periphery of the petiole, and may extend well into the pinnae. They are in close relation with the mechanical tissue, as represented in *fig. 17*.

DISCUSSION

The suppression of one of the cotyledons of *Ceratozamia* illustrates one process by which the monocotyledonous condition may be reached; the fusion of these organs in *Microcycas* affords an illustration of another method, one in harmony with the well-known theory of Miss SARGANT. Experimentation with some of the monocotyledonous dicotyledons listed by COUTLER and CHAMBERLAIN (5) shows that in at least some of them the former process has taken place.

But this fusion of the cotyledons of *Microcycas* has a further meaning to one engaged in the study of a series of juvenile gymnosperms. The free lobing at the tips of the cotyledons in so many cycads seems to me to represent an ancestral condition of polycotyledony. Many embryos of *Zamia* and *Dioon spinulosum* in my collection have four to ten of these lobes, extending, in some cases, three-fourths of the length of the cotyledon. A young embryo of *Dioon spinulosum* with four cotyledons, and one of *Pinus edulis* with twelve cotyledons in four well-marked groups have a remarkable similarity. Of course, the pine cotyledons soon escape from the small, comparatively dry endosperm and thin seed coats, and develop exteriorly to their full

size, which is *in toto* much greater than that attained by the two cotyledons of a cycad. But let the conditions be such as to cause in the pine seed the production of the massive endosperm and indurated coats that characterize the cycad seed; and let the cotyledons be confined within the moist endosperm until they attain their full size, with the pressure of this growth forcing them into such intimate connection with it as to cause difficulty in distinguishing between them, and bringing the tips of the cotyledonary vascular strands into intimate contact with the endosperm, a condition reported by WORSDELL for *Cycas revoluta* (13) and by THIESSEN for *Dioon edule* (12): under such pressure, the inner faces of the pine cotyledons would be very intimately united and the question naturally suggests itself, What would become of the epidermis of these inner faces?

The alternation of mucilage canals with the cotyledonary vascular strands in cycads, and its ready relation to the peculiar condition found in pine cotyledons, may be used as evidence for a theory of fusion as well as for one of splitting, as HILL proposes (8).

The absence of the protostele in the hypocotyl of *Microcycas* in contrast to the condition found in *Dioon edule* and *Ceratozamia* may not have any significance in the light of recent investigation. That the protostele is, in general, the most primitive condition of the vascular axis may be true; but that this structure must occur in every primitive vascular plant is, of course, not true; neither are we to regard as primitive all plants in which it is found. CHRYSLER (4) has found it in members of the Araceae. There are other characters, however, which seem to indicate a greater advance than that made by *Cycas* or *Encephalartos*, or even *Ceratozamia*. These are the single stele and the degree of elimination of the cortical cambium, which, in the cycad stems, produces this vascular tissue. However, the large proportion of centripetal wood in the foliar traces is an offsetting primitive character, which must be weighed in the same balance.

The undoubted polyspermy would seem, at first sight, to bear down the weight of evidence on this side; but it is possible that this primitive feature is a recurrence rather than a direct inheritance: what JEFFREY calls a coenogenetic, rather than a palingenetic, character. JUEL (9) found as many as twenty sperms in the pollen tube of *Cupressus Goveniana*, and no one can believe that *Cupressus* has

retained this primitive feature when all the closely related genera have discarded it.

However that may be, this curious combination of characters, and the absolutely unique archegonial development, are features to be reckoned with by those who, in the future, when all the evidence is in, will be in a position to decide upon the phylogenetic place of *Microcycas*.

What is to be thought of the early appearance of girdling is scarcely worth saying until we learn something definite concerning the cause of girdling itself. The theories now in the field approach only remotely to the causes lying at the foundation of the phenomenon. It is probable that it may be relegated, like so many other problems, to the domain of cytology. That cell division takes place much more frequently in the horizontal than in the vertical direction in every portion of the axis is clearly evident.

SUMMARY

1. There is no resting stage in the development of the embryo of *Microcycas calocoma*.

2. The germination is hypogean.

3. The root is a delayed organ, as in *Dioon* and *Ceratozamia*.

4. There are two cotyledons as in all cycads (except, perhaps, *Encephalartos*).

5. The cotyledons are often fused to form one organic whole, the plumule escaping by bursting the sheath.

6. Mucilage ducts alternate with the 8-10 cotyledonary strands.

7. The cotyledonary node is similar to that of *Dioon edule* and *Ceratozamia*, but the vascular cylinder of the hypocotyl is a siphonostele.

8. The hypocotyl contains no cortical vascular tissue, although there are remnants of a broken-up cambial zone.

9. The vascular strands of cotyledons and leaves are endarch at base and exarch in the upper portions. The exarch condition obtains throughout most of the length of the petiole.

10. Girdling of the marginal leaf traces takes place while the tissue is procambial.

11. The root is tetrarch, but may reduce to triarch toward the tip.

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EXPLANATION OF PLATES V AND VI

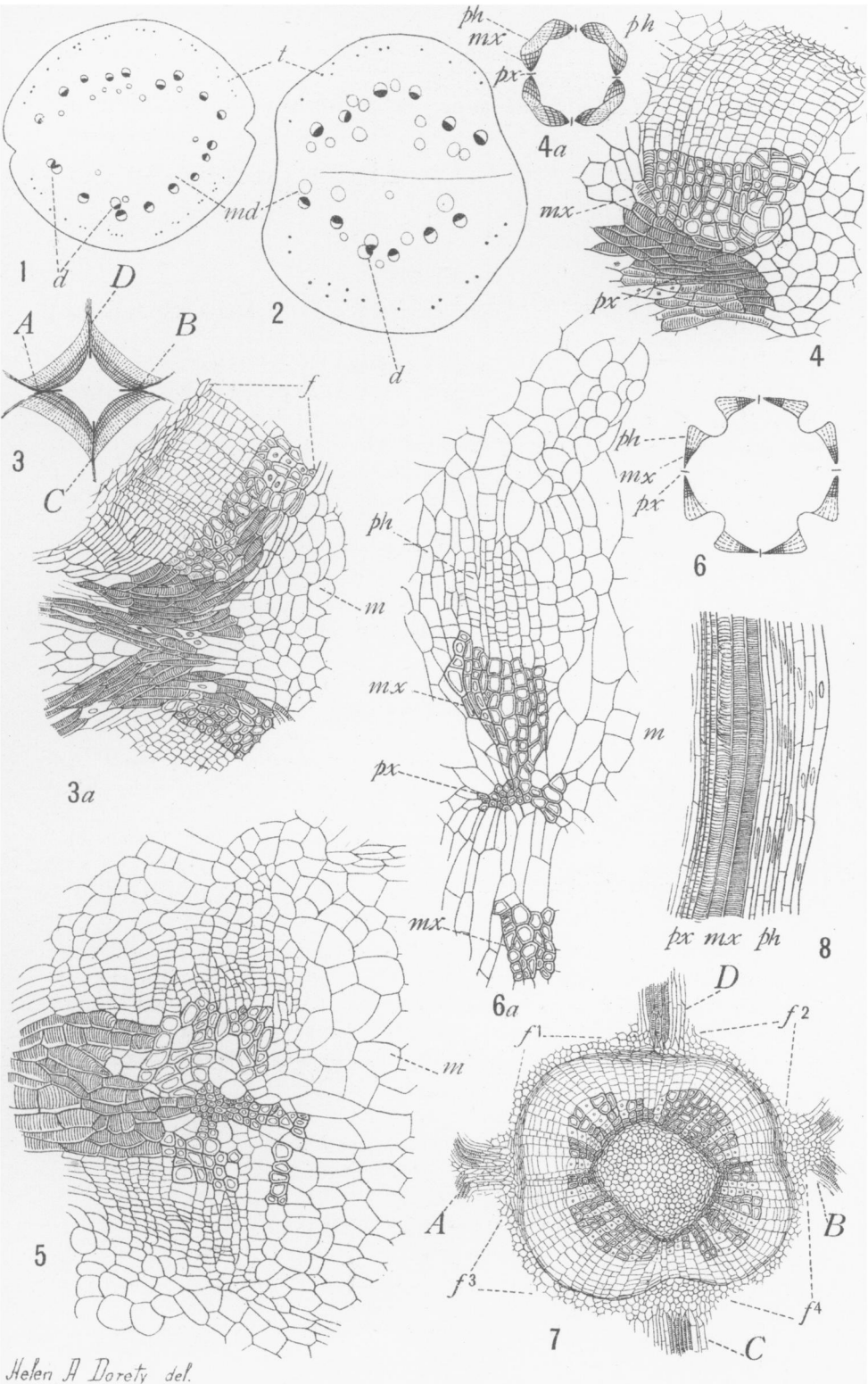
The drawings were made with the aid of an Abbé camera lucida. The following abbreviations have been employed: *A*, *B*, *C*, *D*, main cotyledonary traces; *cs*, cotyledonary sheath; *c/x*, centrifugal xylem; *cpx*, centripetal xylem; *cx*, cortex; *e*, epidermis; *f*, group of leaf traces; *l*, leaf; *m*, medulla; *md*, mucilage duct; *mx*, metaxylem; *ph*, phloem; *px*, protoxylem; *r*, ramentum; *t*, tannin cells.

PLATE V

FIG. 1.—Transverse section near the middle of the cotyledons, showing their complete fusion and the large number of cotyledonary strands. $\times 8$.

FIG. 2.—Transverse section of cotyledons 0.6mm above the tip of plumule. $\times 8$.

FIG. 3.—Diagram of stele 40 μ above the cotyledonary node.



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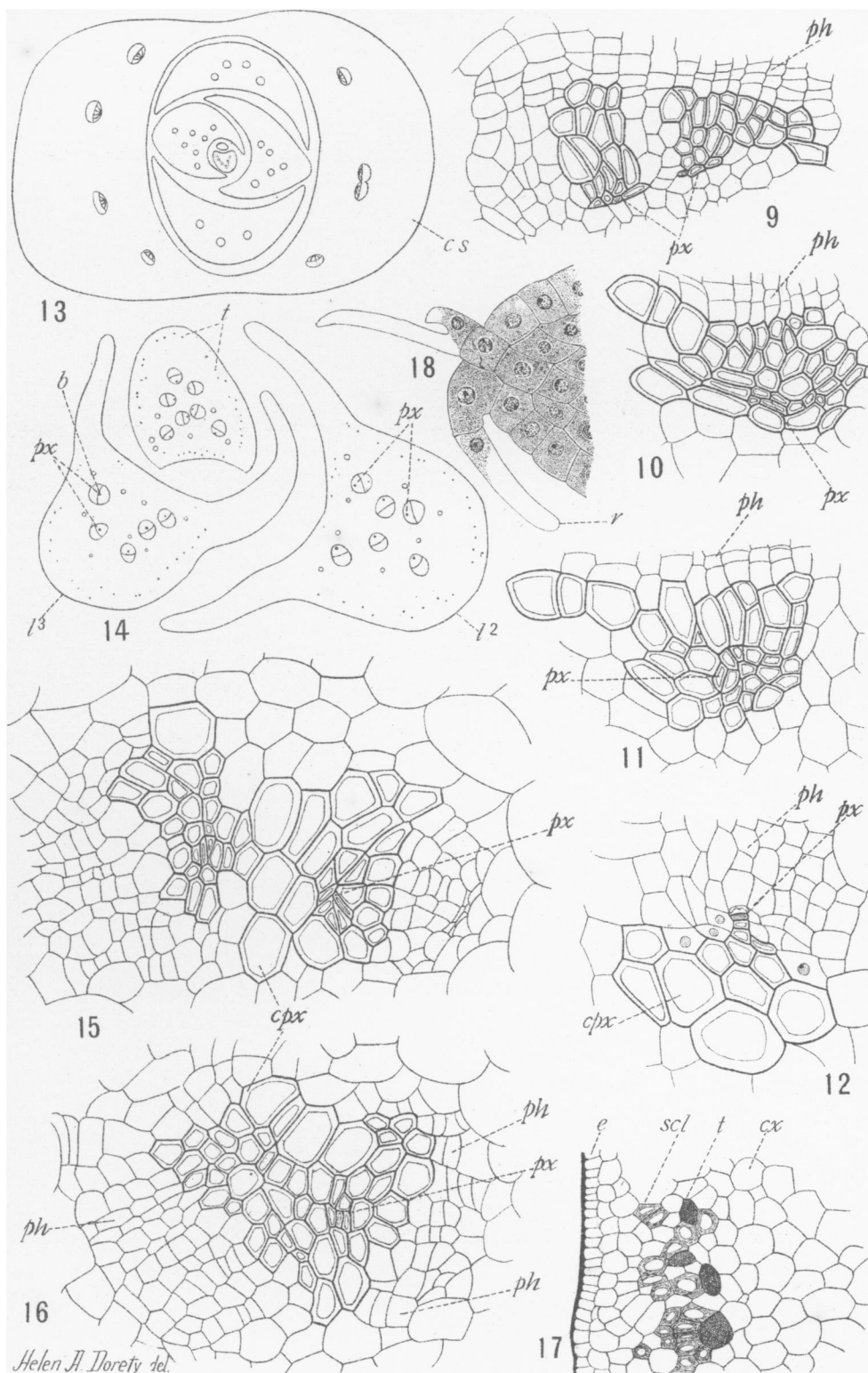


FIG. 3a.—Detail from *fig. 3* showing one of the four cotyledonary traces near its point of insertion. $\times 60$.

FIG. 4.—Base of the cotyledonary trace shown in *fig. 3a*. $\times 60$.

FIG. 4a.—Diagram of stele of hypocotyl showing method of formation of root arrangement.

FIG. 5.—Exit of lateral root. $\times 60$.

FIG. 6.—Diagram of root stele.

FIG. 6a.—Detail of one of the root poles. $\times 60$.

FIG. 7.—Transverse section of the central vascular system above the cotyledonary node. It is composed of four groups of leaf traces. Semidiagrammatic.

FIG. 8.—Longitudinal section of portion of girdling leaf trace taken from transverse section of seedling. $\times 60$.

PLATE VI

FIG. 9.—Transverse section of median traces of same leaf from same section as *fig. 8*. $\times 380$.

FIG. 10.—Transverse section of leaf trace slightly above that represented in *fig. 9*. $\times 380$.

FIG. 11.—Transverse section of same bundle 60 μ above section represented in *fig. 10*. $\times 380$.

FIG. 12.—Exarch bundle from petiole 8^{mm} from base. $\times 380$.

FIG. 13.—Transverse section of embryo, showing the sheath formed by the fusion of the cotyledonary petioles, the increase in the number of leaf traces in consecutive leaves, and their gradual assumption of the Ω arrangement. $\times 8$.

FIG. 14.—Transverse section of three leaves in their natural arrangement, showing the relative amount of centrifugal wood at different levels of the petiole. $\times 8$.

FIG. 15.—Approach of two leaf traces. $\times 380$.

FIG. 16.—Fusion of some of the xylem elements of same to form a quasi-concentric strand. $\times 380$.

FIG. 17.—Portion of peripheral region of tissue of petiole showing position of tannin cells. $\times 380$.

FIG. 18.—Tip of young pinna showing unicellular hairs or ramentum. $\times 760$.